Seasonal xylem pressure potentials of two South African coastal fynbos species in three soil types

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The seasonal dawn and midday stem xylem pressure potentials of two South African coastal fynbos species, *Thamnochortus punctatus* and *Leucospermum parile* growing in three soil types were measured from July 1981 to May 1982. The results show that the response of the two species was markedly different; the deeper rooted *L. parile* exhibited little or no moisture stress throughout the year while the decreasing spring-summer (September-March) potentials of the shallow-rooted *T. punctatus* suggest a degree of water stress in summer. The potentials of *L. parile* are high by comparison with those of other mediterranean shrubs, but both rainfall and shoot growth data suggest that the summer drought period studied was not extreme. *L. parile* appears to conform to Specht's (1972) concept of a water-conservative, mediterranean, evergreen sclerophyll. P.C. Miller (pers. comm. 1981) who died unexpectedly in 1982 before much of his fynbos data was published, suggests that restioids, including *T. punctatus*, employ a 'boom or bust' water strategy, using a lot of water when it is available and conserving it when it is scarce; these data support this concept. In terms of soil type the observed differences in the xylem potentials of both species can be explained by differences in soil water-holding capacity.

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Die seisoenale dagbreek- en middag-stamxileem-drukpotensiaal van twee Suid-Afrikaanse kusfynbos-soorte, *Thamnochortus punctatus* en *Leucospermum parile*, wat in drie grondtipes voorkom is van Julie 1981 tot Mei 1982 gemeet. Die resultate toon dat die reaksie van die twee soorte merkbaar verskillend is; die dieper-gewortelde *L. parile* het min of geen vogtekort dwarsdeur die jaar getoon nie terwyl die verminderde lente-somer (September-Maart)-potensiale vir die vlak-gewortelde *T. punctatus* 'n graad van vogtekort in die somer suggereer. Die potensiale van *L. parile* is hoog in vergelyking met dié vir ander mediterreense struike, maar beide reënval en lootgroeidata suggereer dat die somerdroogteperiode wat bestudeer is nie baie droog was nie. *L. parile* skyn aan Specht (1972) se konsep van 'n waterbewarende, mediterreense, immergroen sklerofiel te voldoen. P.C. Miller (pers. mededeling, 1981) wie onverwags in 1982 gesterf het voor veel van sy fynbos-data publiseer kon word, stel voor dat restioïede, insluitende *T. punctatus* 'n 'maak of breek'-strategie aanwend deur baie water, wanneer dit beskikbaar is, te gebruik en dit te bewaar wanneer water skaars is; hierdie data ondersteun dié konsep. In terme van die grondsoorte kan die waargenome verskille verduidelik word in terme van die verskille in grond-waterhouvermoëns.

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Introduction

A mediterranean climate, as experienced at the study area in the southwestern Cape region of South Africa, characteristically includes some degree of summer drought (Schulze & McGee 1978). The aim of this study was to investigate the response of the stem xylem pressure potential of two species with different rooting depths to the summer period of assumed moisture stress (Kruger 1979). Several authors have noted that Californian and Chilean mediterranean shrubs with deeper root systems experience less water stress, evidenced by higher xylem potentials, than do shallow-rooted shrubs (Morrow & Mooney 1974; Poole & Miller 1975; Riveros *et al.* 1976; Krause & Kummerow 1977; Burk 1978; Giliberto & Estay 1978; Schlesinger & Gill 1980; Roberts *et al.* 1981; Miller 1982). More specifically, Roberts (1982) reports a 1 – 1,5 MPa reduction in the water potential of *Quercus agrifolia* Neé. on the removal of 70% of the lateral roots. In Australian heath communities Groves & Specht (1965) found that roots were deeper in dry than in wet soils and that community water relations were affected by root depth (Specht & Jones 1971). However, Hanes (1965) found that the shallow-rooted Californian redshank (*Adenostoma sparsifolium* Torr.) appeared to be less water stressed and grew during spring to summer, in comparison with the deeper-rooted chamise (*Adenostoma fasiculatum* H. & A.), which grew in late winter to spring.

A further aim of this study was to investigate the effects of soil type on the xylem pressure potential of the species. Barnes & Tyrone Harrison (1982) found marked differences in the seasonal distribution and availability of moisture in the coarse upper dune sands and finer lowland soils of the Nebraska sandhills. In comparison with the finer soils there was more moisture available throughout the sandy profile during the dry summer-autumn period. In the finer soils, on the other hand, more moisture was available near the surface during the wet winter-spring period.

Study areas

The study areas were at Pella, the Sand Plain Lowland Fynbos (Moll *et al.* 1984) intensive study site for the C.S.I.R. Fynbos Biome Project, located 35 km NE of Cape Town at 33°31′S, 18°32,5′E. The vegetation is dominated by evergreen, sclerophyllous species representing the three characteristic fynbos elements: the proteoid, ericoid and restioid (Taylor 1978; Kruger 1979). The study areas were situated in five-year-old *Leucospermum parile-Stoebe leucocephala, L. parile-Thamnochortus punctatus* and *Diastella proteoides-Berzelia abrotanoides* communities (Boucher, in prep.).

Figure 1 illustrates the monthly rainfall and absolute maximum and minimum air temperatures from June 1981 to May 1982, collected at the Pella weather station. The rainfall data are compared with the 49-year average from the nearest Weather Bureau Station, at Burgherspost (33°30′S, 18°32′E). The soils at Pella are aeolian sands; a catena of five soil types exists, with two seasonally-waterlogged types completing the seven major types. The soil forms investigated were the Hutton, Clovelly and Westleigh, or more specifically the Alloway, Lismore and Chinde series of these forms, respectively (MacVicar *et al.* 1977). The Hutton soil at the head of the catena has a high iron content and is a well-drained, red, medium sand which is usually associated with a relatively high water-holding capacity. The Clovelly, having a lower iron content, is intermediate on the catena and is a yellow, medium sand with an intermediate water-holding capacity. The Westleigh is a grey, slightly coarser, medium sand which exhibits soft, plinthic mottling within 300 mm of the surface, indicating that waterlogging has occurred in the past.

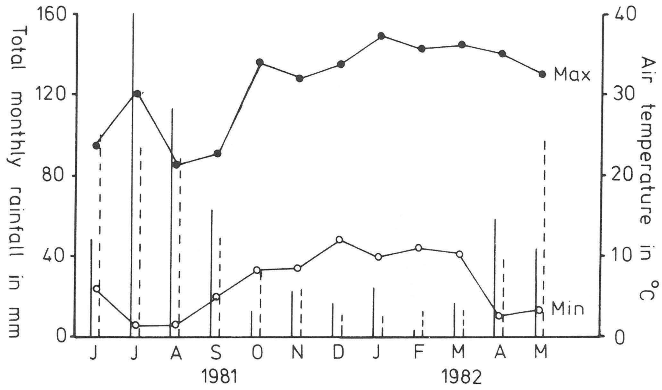

Figure 1 Monthly rainfall (|) and absolute maximum and minimum air temperatures (●; ○) at the Pella climate station during the study period. Forty-nine-year mean monthly rainfall from Burgerspost (¦).

Materials and Methods

Study species

The two species studied, *Leucospermum parile* (Salisb, ex Knight) Sweet and *Thamnochortus punctatus* Pillans, were selected because of their widespread abundance at the study site and the consequent concentration of plant-nutrient, -litter and -phenology studies on these species. *L. parile*, a member of the Proteaceae, is an 'erect to semi-erect, rounded shrub up to 1,5 m in height, with a single stout main stem. The leaves are covered with a short, dense, canescent indumentum of short crisped hairs' (Rourke 1972). It has an extensive tap root system concentrated in the upper 600 mm but extending to below 2 m. *Thamnochortus punctatus* belongs to the most characteristic fynbos family (Taylor 1978), the Restionaceae, '. . . a very old Southern Hemisphere family found chiefly in South Africa and Australia.' (Levyns 1966). The Restionaceae are usually dioecious, perennial rush or sedge-like, evergreen hemicryptophytes with photosynthetic stems and the leaves are reduced to papery sheaths at the nodes; some species have finely divided barren branches made up of both stem and leaf material. *T. punctatus* (Figure 2) has caespitose, erect, simple stems, some of which bear barren branches; the male spikelets are numerous and in lax, panicled cymes 12 – 20 mm long (Pillans 1928). The male plants sampled were 700 – 800 mm in height with densely branched rhizomes and shallow, fibrous root systems, some 300 mm deep, but concentrated in the upper 100 mm of soil.

Figure 2 Sketch of part of a six-year-old male *Thamnochortus punctatus* plant. (a) Fibrous roots; (b) rhizome; (c) photosynthetic culm; (d) papery leaf sheath; (e) barren branch; (f) mature inflorescence.

Shoot xylem pressure potential

Xylem pressure potentials were measured using the pressure chamber technique (Scholander *et al.* 1965). These measurements are assumed to approximate closely the total xylem pressure water potential since the solute and matrix components of water potential are constant or negligible in most non-halophytic plants (Boyer 1969; Kappen *et al.* 1972). Measurements were made on at least two of the current years shoots on a single individual of both *L. parile* and *T. punctatus*, the number being increased to provide a more representative range when high variability was encountered in the readings. At the same time the number was limited to reduce the time elapsed between readings on plants in the three soil types. Plant size, shoot age and height were comparable throughout the investigation, thus avoiding these sources of variation (Waring & Cleary 1967; Ritchie & Hinckley 1975). The time that elapsed between cutting a shoot and measuring the xylem pressure was kept to a minimum while the rate of increase of air pressure was kept relatively constant to reduce errors owing to these factors (Waring & Cleary 1967; Ritchie & Hinckley 1975). Measurements were made as close to dawn and midday as possible to compare the plants' responses to soil moisture and evaporative stress, respectively (Oberbauer & Billings 1981). Measurements were made at approximately monthly intervals from July 1981 on *L. parile* and from September 1981 on *T. punctatus*, once the shoots were long enough to be measured, and continued until May 1982.

Soil moisture

Gravimetric determinations of soil moisture were carried out on ± 50-g soil samples of each soil type collected with a soil-corer at depths of 0 – 50, 100 – 150, 350 – 400 and 750 – 800 mm. Four replicates were collected at each depth on each sampling date. Soil temperature was measured at approximately midday using Wescor thermocouple psychrometers buried at approximately 50, 150, 400, 800 and 1000 or 1500 mm in each soil type.

Veihmeyer & Hendrickson (1950) question the reliability, both of measurements made from soil samples and from instruments buried in the soil, because the absorbing portions of plant roots do not always thoroughly permeate the soil. They advocate the use of the predawn maximum xylem pressure potential as an approximation of 'effective soil moisture'. But, as soil moisture availability decreases and daily evaporative stress increases, plant equilibration time increases so that plant predawn potential diverges from soil moisture availability (Ritchie & Hinckley 1975).

Results

In *L. parile*, dawn potentials of plants in all three soil types, presented in Figures 3a, b & c, were high and relatively constant. There was a slight increase during winter-spring; from July-August (– 0,17 to – 0,32 MPa) to October (– 0,02 to – 0,08 MPa). This was followed by a general decrease from October to February (– 0,17 to – 0,5 MPa) interrupted in both the Clovelly and Westleigh, and to a lesser degree in the Hutton soils, by an increase in the January values. The lower potentials in the Clovelly soil in February (– 0,5 ± SE 0,03 MPa) were probably the result of the measurements being made nearly two hours after dawn. Finally the potentials increased during Autumn; February to May (0 to – 0,05 MPa). The midday potentials were lower and exhibited an overall decrease from July (– 0,42 to – 0,46 MPa) to February (– 0,69 to – 0,86 MPa) followed by an increase, which was most marked in the Hutton soil from February to May (– 0,12 to – 0,48 MPa), comparable to the trend in the dawn potentials.

There was an overall decrease in *T. punctatus* dawn potentials (Figure 4) during spring and summer; from September (– 0,1 to 0,13 MPa) to February and March (below the – 4 MPa limit of the pressure gauge). As in *L. parile* this decrease was interrupted in all three soil types by higher potentials in January. Potentials increased dramatically from March to May (– 0,03 to – 0,17 MPa). Midday potentials were lower but exhibited similar trends to the dawn potentials, although the increase in the January potentials was less marked in both the Clovelly and the Westleigh soils. In addition, midday potentials decreased more rapidly in the Hutton than in either the Clovelly or the Westleigh soils.

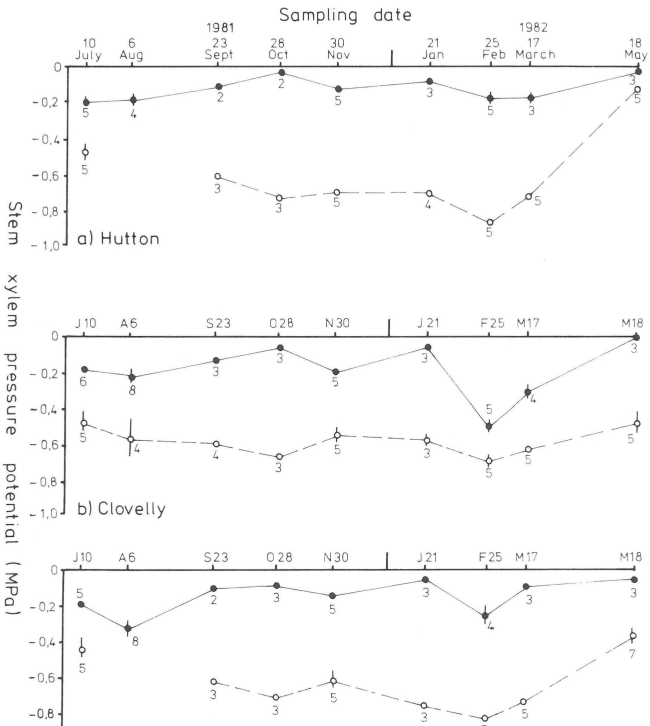

Figure 3 Seasonal dawn (●) and midday (○) mean (± SE) stem xylem pressure potentials of *Leucospermum parile* in the Hutton (a), Clovelly (b) and Westleigh (c) soil types (sample size is indicated on the graph and varied from 2 to 8).

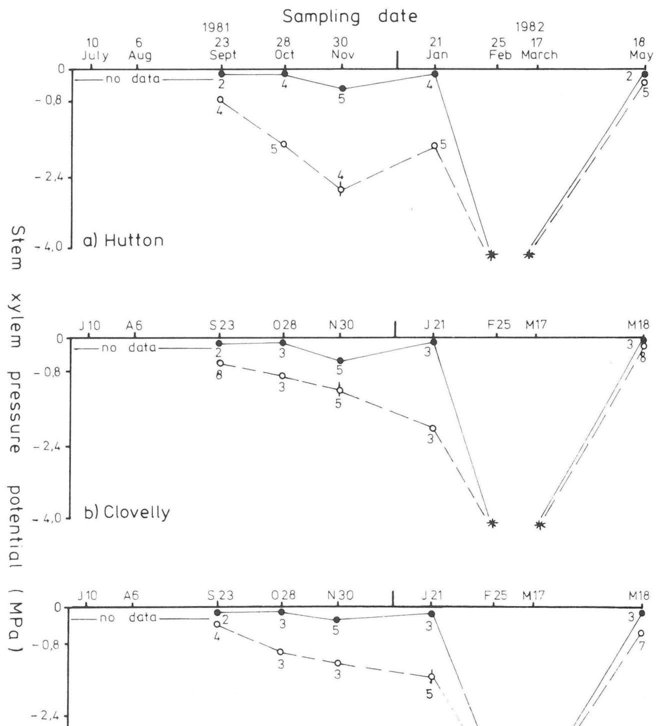

Figure 4 Seasonal dawn (●) and midday (○) mean (± SE) stem xylem pressure potentials of *Thamnochortus punctatus* in the Hutton (a), Clovelly (b) and Westleigh (c) soil types (sample size is indicated on the graph and varied from 2 to 8. * – 4 MPa pressure guage limit.

The gravimetric soil moisture data (Figure 5) illustrated the progressive drying out of all three soil types from August to March and their rehydration by May. The increase in moisture in the surface layers in January was more marked in the Hutton than in either the Clovelly or the Westleigh soils. The soil temperature data (Figure 6) show slight increases from November to February and decreases from February to May which are most marked in the upper soil surface.

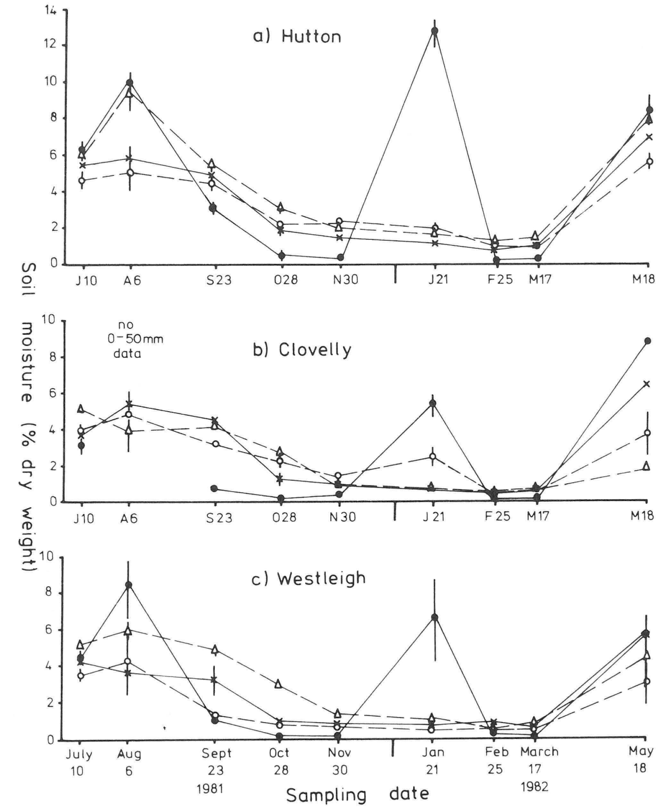

Figure 5 Seasonal gravimetric soil moisture content of the Hutton (a), Clovelly (b) and Westleigh (c) soils at 0 – 50 mm (●), 150 mm (○), 400 mm (×) and 800 mm (△), mean of four samples ± SE.

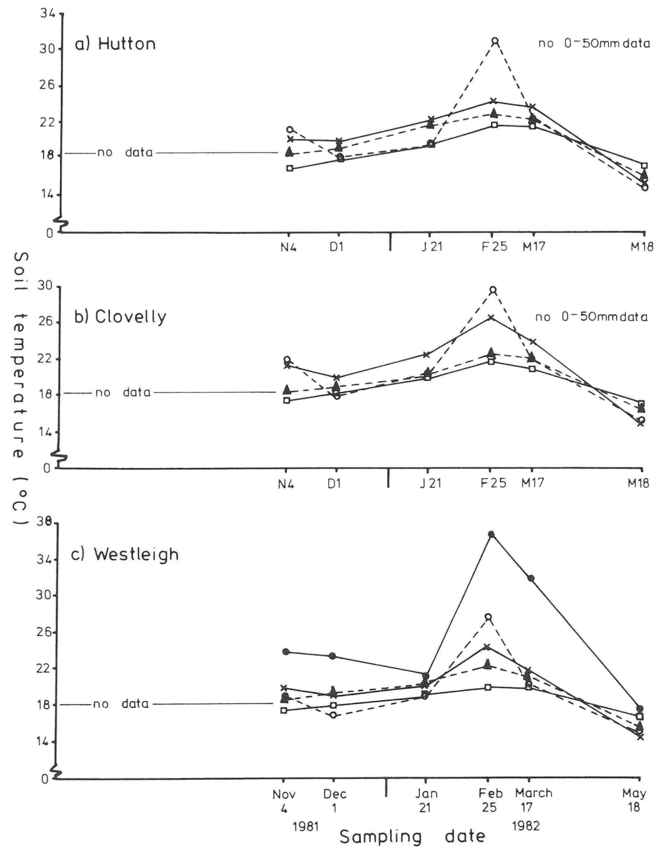

Figure 6 November 1981 to May 1982 soil temperatures in the Hutton (a), Clovelly (b) and Westleigh (c) soils at 0 – 50 mm (●), 150 mm (○), 400 mm (×), 800 mm (△) and 1000 or 1500 mm (□), mean of four samples ± SE.

Discussion

The seasonal xylem pressure responses of the two species was markedly different. The magnitude and relative constancy of the deeper-rooted *L. parile* xylem pressure potentials throughout the study period suggest little or none of the assumed summer water stress. The moderate leaf conductances and xylem pressure potentials measured by J.M. Miller *et al.* (pers. comm.) on *L. parile* in November and December 1981 support this. *L. parile* potentials may be compared with those of three species of *Rhus* from Californian chaparral which were – 1 MPa at dawn and the daily minimum not less than – 2 MPa throughout the year (Poole & Miller 1981). Two Chilean matorral species, *Lithraea caustica* (Mol.) Hook & Arn. and *Quillaja saponaria* Mol., exhibited minimum values of greater than – 2,5 MPa (Giliberto & Estay 1978). But, these potentials are lower than the 0 to – 0,32 MPa dawn and – 0,12 to – 0,86 MPa midday potentials we recorded for *L. parile*. The highest xylem pressure potentials we have seen quoted for mediterranean, evergreen shrubs were – 0,5 MPa at dawn and a minimum of – 2 MPa for *Ceanothus velutinus* Dougl. ex Hook. and *Arctostaphylos patula* Greene in montane chaparral (Conrad & Radosevich 1981). However, it is obvious from the literature that xylem pressure potentials can vary tremendously with severity of drought, e.g. Parsons *et al.* (1981) data for *Arctostaphylos viscida* Parry. A comparison of the rainfall during the study period with the 49-year mean (Figure 1) shows that there was above average winter (July and August) and mid-summer (January) rainfall, suggesting perhaps that the 1981 – 1982 drought was not severe and thus accounting for the high potentials in *L. parile*. The similarity between the timing of *L. parile* shoot growth in the three soil types in 1981 – 1982, by comparison with the significant differences in 1980 – 1981, is consistent with this (Sommerville 1983).

T. punctatus, with its shallow root system, exhibited a degree of moisture stress evidenced by the low potentials observed in February and March. The decrease in dawn and midday xylem pressure potentials from September to February and March corresponds with a decrease in gravimetric soil moisture. The increases observed in January may be attributed to the unusually high rainfall that month (Figure 1), with 6,9 mm falling on the sampling day and 9 mm the day before. The September to January dawn potentials remained relatively high, suggesting that during this period the plants were able to equilibrate overnight from the increasing daytime stress. But in February and March both the midday and, more markedly, the dawn pressure potentials decreased dramatically from – 0,15 MPa to less than – 4 MPa, indicating little or no overnight equilibration. This dramatic decrease in xylem pressure potential is not paralleled by air temperatures (Figure 1), soil moisture (Figure 5) or the values measured on *L. parile* (Figure 3). A study of the seasonal changes in above and below-ground phytomass of *T. punctatus* showed that the young roots formed during winter-spring had shed their absorptive cortex by summer (Sommerville & Stock, pers. obs.). Presumably the cortex is shed above a certain level of moisture stress during summer, probably rendering the roots non-absorbent. This could account for the sudden decrease in both dawn and midday xylem pressure potentials. An investigation of another species of Restionaceae at Pella, *Cannamois acuminata* (Thunb.) Pill., showed that a thick cuticle develops on the culms at the same time that the root cortex sloughs off under conditions of water stress (J. Hardcastle, pers. comm.). If this thick cuticle develops in *T. punctatus* the low pressure potentials may be a measure of the resistance of the culms to gas exchange rather than a measure of the xylem pressure potential. The growth of new absorptive roots combined with increased soil moisture accounts for the high potentials measured in May (Sommerville & Stock, pers. obs.).

Unfortunately midday xylem pressure potentials for *T. punctatus* cannot be directly compared with those for species in other mediterranean regions because of the limits of our pressure gauge and the lack of data for comparable growth forms. J.M. Miller *et al.* (pers. comm.) have comparable data for *T. punctatus* at Pella in November and December. Their data for other restioids are rather variable and they attribute this to differences in root depth and phenology. With reference to the low dawn potentials in *T. punctatus* several species of mediterranean shrubs have exhibited some overnight recovery from minimum potentials of less than -4 MPa (Poole & Miller 1975, 1981; Burk 1978; Baker *et al.* 1982). *Cryptocarya alba*, on the other hand, showed little or no recovery from potentials of only $-3{,}4$ MPa (Riveros *et al.* 1976).

One of the most obvious differences between *L. parile* and *T. punctatus*, which may account for the differences in xylem pressure potential and implied water stress, is the depth and extent of their root systems. Our data agree with those for many other mediterranean shrub species, with the deeper rooted *L. parile* exhibiting lower xylem pressure potentials than the shallow rooted *T. punctatus*. However, it is unlikely that xylem pressure potential is controlled by a single factor such as root depth and two other major areas of influence are identified in the literature. Leaf orientation, size and anatomy affect xylem pressure by their influence on leaf exposure, temperature and water loss (Mooney & Kummerow 1971; Harrison *et al.* 1974; Morrow & Mooney 1974; Riveros *et al.* 1976; Burk 1978). The photosynthetic organs of the two species studied are very different; *L. parile* has leaves with a dense layer of surface hairs which probably reduce water loss and *T. punctatus*, on the other hand, photosynthesizes largely through erect, cylindrical culms which are probably less exposed to sunlight; they also have deeply sunken stomata (J. Hardcastle, pers. comm.). Secondly, the physiological control of transpiration, photosynthesis and stomatal closure affects xylem pressure potential (Hanes 1965; Harrison *et al.* 1974; Riveros *et al.* 1976; Ng & Miller 1980; Poole & Miller 1981). No data are available on the physiological responses of *L. parile* and *T. punctatus* and in particular on their tolerance of low xylem pressure potentials; a feature which Ritchie & Hinckley (1975) emphasize as an important constraint on direct comparisons of water stress of species, based on xylem pressure potentials.

Although the gravimetric soil moisture data show few marked, consistent differences between soil types, plant-available moisture levels were probably considerably different. The high water-holding capacity normally associated with the high iron content and small particle size characteristic of Hutton soils would make plant-available moisture levels lower than those of the coarser-grained, lower iron-containing Clovelly and Westleigh soil types. There were some isolated differences in the responses of both species in the three soil types. The increases in the January dawn potentials of *L. parile* in both the Clovelly and the Westleigh soils were not observed in the Hutton soil. This may be explained by the assumed higher water-holding capacity of the Hutton, as evidenced by the soil moisture data (Figure 5a). The increase owing to the rain on and prior to the sampling date was confined to the 0 – 50 mm layer so that little moisture percolated through to the *L. parile* roots deeper down. The lower moisture contents of the upper 50 mm in both the Clovelly and the Westleigh soils and the increase of moisture in the 150 mm Clovelly samples suggest that the rain had percolated deeper in these soil types. We have no evidence to explain the slightly lower midday potentials that occur throughout most of the year in both the Hutton and the Westleigh soils, nor for the appreciably lower potentials occurring in the Hutton soil in May.

Midday *T. punctatus* potentials in the Hutton soil differed from those in both the Clovelly and the Westleigh soils during the September-January period (Figure 4). Firstly, the Hutton potentials decreased more rapidly, presumably as a consequence of the higher water-holding capacity of this soil as discussed above. Further, the increase observed in the January potentials was most marked in the Hutton soil, probably because more water was retained in the 0 – 50 mm layer (Figure 5) and because *T. punctatus* roots are largely confined to the 0 – 100 mm layer.

Conclusions

From these data it appears that *L. parile* did not experience the assumed summer moisture stress (Kruger 1979) while *T. punctatus* exhibited increasing moisture stress during spring and summer. This difference in response may be explained in terms of differences in rooting depth and extent, photosynthetic organs and physiological response.

Californian chaparral has been divided into: Dry areas receiving less than 500 mm rainfall per annum with a predominance of species with high leaf conductances, variable seasonal water potentials, shallow roots and seed regeneration. The wetter areas receive more than 500 mm of rain and their species have lower leaf conductances, relatively constant water potentials, deep roots and regeneration from the rootstock (Miller 1981). *T. punctatus* exhibited moderate leaf conductances (J.M. Miller *et al.*, pers. comm.) but otherwise conformed to the description of a dry area species. *L. parile* exhibited moderate leaf conductances and seed regeneration in combination with stable water potentials and deep roots so that it does not completely fit either the wet or the dry species description, which is not surprising considering that the Burgerspost 49-year rainfall mean is 555 mm. From this study and data on leaf conductance and stem xylem pressure potential (Miller *et al.* 1983), it appears that proteoids, including *L. parile*, conform more closely to Specht's (1972) concept of a water-conservative mediterranean shrub with high, constant seasonal xylem pressure potentials, moderate leaf conductances and growth continuing through spring to summer. Specht maintains that many Australian species have high temperature requirements for growth owing to their tropical origin; for growth to occur during summer these species must use water conservatively. Miller & Poole (1979) argue that conservative water use may be possible in pure stands but not in mixed stands owing to competition. Data for *Adenostoma fasciculatum* in pure and mixed stands on different slopes lend some support to their argument (Roberts *et al.* 1981).

P.C. Miller (pers. comm.) suggests that restioids such as *T. punctatus* employ a 'boom or bust' strategy involving high water use when water is abundant and conservative use when water is scarce. This may in turn be related to the shallow rooting depth of these species. The high transpiration rates under non-stressed conditions, contrasted with the formation of a thick stem cuticle layer and the sloughing of the root cortex under conditions of moisture stress in *Cannamois acuminata*, support this concept (J. Hardcastle, pers. comm.).

Differences in soil moisture in the three soil types were not as marked as those in the soils of the Nebraska sandhills. It is possible that the methods used for measuring both plant and soil moisture were not sufficiently sensitive and sampling was too infrequent to adequately illustrate differences. But from both the high xylem pressure potentials in *L. parile* and the rainfall data it appears that the 1981 – 1982 summer drought period was not severe, which would make differences in moisture stress less obvious. The similarity between the timing of *L. parile* shoot growth in the three soil types during the 1981 – 1982 growth season compared with the significant differences in 1980 – 1981, is consistent with this hypothesis (Sommerville 1983).

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